

## SOME BASIC PRINCIPLES OF INSECT WING VENATION

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The two things primarily involved in the making of the venation of insect wings are hypodermis and tracheæ. Two other things are present: blood, bringing food and removing wastes, here as elsewhere; and nerves, maintaining lines of communication between all peripheral parts and the control centers. But blood is a fluid, and nerves are tissue lines of excessive tenuity and softness; and I know of no reason for thinking that either has anything to do directly with determining the pattern of the venation.

### 1. TRACHAE

I begin where veins begin, with tracheæ. In the nymphal wings of all the more generalized insects tracheæ grow out first and later the veins are developed about them. When the two layers of the wing sac fuse to form the wing membrane, the cylindric, tænidia-lined tracheæ keep them apart as passage-ways for blood and air.

Tracheæ lay down the pattern of the long veins. It is at first a simple pattern of gently undulating forks, but later it becomes complicated by conjunctions and by shifting. The veins of many of the oldest fossil insects, the Palaeodictyoptera, run across the wings forking quite after the manner of tracheæ, in relative independence and without strong cross connections.

In the nymphs of stoneflies whose wings are of the simplest sort, externally developing and growing to relatively large size, the correspondence between veins and tracheæ is very close, extending to almost every detail. It is only a little less close in other insects whose wings develop freely to the outside. Deviations from this correspondence are for cause. Tracheæ in their development tend to follow ancestral paths in absence of anything to turn them aside; and the veins continue to be laid down on the same old lines even after tracheæ have been suppressed.

The insect wing begins as the fold of skin, not very different

from the fold that occurs whenever the margin of one segment overlaps another segment. This low broad fold elongates and becomes triangular as it extends to rearward, increasing in size with each successive moult. Always it is a simple flattened sac, containing no viscera. Its lumen is an extension of the body cavity. The blood of the body enters and brings it food. Tracheæ enter and bring its tissues oxygen.

Moulting, which allows for expansion of the external cuticle, also allows for extension of the tracheæ; for at each moult the gas contained in the lining of the trachea is withdrawn with that lining from the body. The soft tracheal walls are for the time being filled with fluid. Re-inflation follows. Gases forming in the tissues are taken up first in some of the larger tracheal trunks. As the increasing volume of gas pushes each way along the trunk and into the branches it enters the wing and fills out and extends, more completely with each moult, those tracheæ which will compose the final pattern.

Tracheæ enter the wing bud from two sources, front and rear. It is probable that in the beginning the branches were numerous, and that a struggle for existence occurred among them like that of the sprouts of the stump of a felled tree—a struggle for place and standing room. Those most advantageously situated were near the middle of the wing, where the outward extension of the wing sac is greatest, and where the crowding of the corners is least. At any rate the middle tracheæ of the wing, R, M, and Cu, remain the largest and most regular in their type of branching. They constantly recur in like number, form, and relation, and so, bear the usual earmarks of homology.

The two primary groups of tracheæ have remained separate in nymphs of Plecoptera, and of some of the Blattidæ. In most insects they are conjoined by a basal anastomosis into one common alar trunk from which all the wing tracheæ arise. Two groups are still indicated by their basal curvature; an anterior costo-radial group, and a posterior cubito-anal group, with the median trachea, originally a member of the former group, vacillating between. It was the discovery of this fundamental tracheal plan that brought the interpretation of the venation of the orders Plecoptera, Orthoptera, Corrodentia, Hemiptera,

Neuroptera and Lepidoptera into line, and placed the system upon a firm morphological basis.

The wings of insects are of extraordinary diversity, and it is not surprising that they differ in tracheation. In order to find primitive conditions it is necessary to study the more generalized members of each order; for, with specialization, tracheæ, like other organs, may be diverted or even largely suppressed. The costal trachea early disappears and at both edges of the wing base tracheæ tend to be conjoined.

When the growth of the wing is retarded as in complete metamorphosis, the entrance of the tracheæ is delayed. Wing buds ("imaginal discs") of microscopic size, retained beneath the larval skin, are adequately supplied with air by tracheoles. These spring from adjacent tracheæ and press for entrance at the base of the incipient wing fold in tangled skeins. They "storm the doors" so to speak; but there is as yet no standing room inside. Only when the wing bud is released by the loosening of the larval cuticle is there space within the fold that tracheæ may enter. Tracheæ are open tubes that must not be compressed if they are to fulfill their respiratory function.

Even with complete metamorphosis there is gradation. In the Sialidæ the correspondence between veins and tracheæ is very close. All grades of diversion may be found in the Lepidoptera, while in the Diptera and several other orders tracheation is so modified as to be of no aid in determining homologies. In all such specialized forms wing growth is greatly retarded. The larval wing buds are very minute. Vein development is begun before the tracheæ can enter, the wing base is narrow, and the wing sac is open so that they are quite free to wander. All that remains of their primitive arrangement is their proceeding from two sources of the wing base.

That this should be true of the Trichoptera is not surprising when we remember that the wing buds of the larvæ are minute: they develop under the protection of the caddis; and the two layers of the wing sac remain apart until long after the tracheæ have entered. The more generalized Trichoptera have a venation pattern almost identical with that of certain Jugate Lepidoptera which have the tracheation complete and normal.

An effort has been made to cast doubt upon the validity of all evidence from tracheæ because of the fact that they are of no use in determining homologies in the Trichoptera. It is as if a mammalogist were to say that because whales have no teeth, phylogenetic evidence from mammalian dentition may be disregarded.

## II. HYPODERMIS

The chitin of the wing is produced by the hypodermis, and in the beginning this does not differ from that of the adjacent body wall. The wing is in origin an outgrowing fold. As its surface expands chitin tends to be condensed around the tracheæ, forming veins. Between the tracheæ it forms a meshwork of irregular ridges enclosing areoles of thinner membrane. This is the *archedictyon*, or ancient network of Tillyard.

An archedictyon filled the interspaces in the wings of the most ancient fossils. It is still present in some Megaloptera, in the tegmina of many Locustidæ, and in the less expanded parts near the base of the wing in other Orthoptera. Net-veined expansions of cuticle occur elsewhere than on wings; as, for example, in the flat lateral prothoracic plates of the Tingitidæ. Clearly the archedictyon is primitive.

The two hypodermal layers of the developing wing sac are at first separate, but they become fused together as development proceeds. Fusion first occurs midway of the tracheal interspaces. It gradually spreads until the tracheæ are inclosed in well-defined channels. Blood circulates in these channels and nerves lie in their walls. About them the chitin thickens to form the principal veins. Cross channels between them, at first irregular and containing only tracheoles, become the crossveins.

Hypodermis builds the veins. It builds them in the beginning around tracheæ; and at the last, even when tracheæ have been crowded out or retarded and shifted, it builds them into a framework that has for its basis the old tracheal pattern.

Vein building is a process of selective scleritization. The hypodermis at the later moultings deposits its hard substances in veins and crossveins, leaving the interveing membrane thin. It first encloses the tracheæ where they lie, and then it bends them into the shape of the veins that are to be, and binds them with

strong chitinous braces. Thus it puts the strength-giving material of the wing into positions of mechanical advantage. Often it binds adjacent parts of two tracheæ into a single vein.

Hypodermis builds the basal articulations of the wing. There was skin before there were sclerites. Selective deposition of the harder material made the basal sclerites and the apodemes thick and left the sutures between them thin: thin and resilient.

### III. WING SHAPING

Insect wings may have developed from parachute-like expansions of the thoracic wall, which once served only for gliding. To become wings these glider planes would have to become articulated at the base and narrowed and strongly supported there. Muscles that once served for adjusting the inclination of the planes might become adapted to moving the wings up and down.

Situated as wings are at the middle of the segments, the pleural apodeme would naturally come to be their chief fulcral point. The strongly conjoined costo-radial group of veins stands rigidly above this point. To rearward extend the islets of scleritization called axillary sclerites, and the basal thickenings of the cubito-anal veins.

The wing is still a narrow fold of the body wall, and to keep it in line for proper action it is anchored at front and rear: forward by means of tegulæ; rearward, by means of the axillary cord. Between these strong and flexible stays it swings freely, not as on a long hinge in a fixed plane but with a relatively fixed rotation at the front about the head of the apodeme, and with freedom of adjustment to the rear. The adjustment of the planes is by the pull of the muscles about the wing base.

No profound knowledge of mechanics is required for an understanding of the operation of the insect wing, but only a little careful observation of its structure and action. Whatever its venation pattern, the wing is stiff and rigidly supported at the front, and pliant and rather loosely slung in the rear. When vibrated up and down the stiff front edge cuts the air: the broad yielding hinder plane glides upon it. The action is that of sculling, the obliquity of the wing strokes alternately up and down resulting in forward progress.

Fore and hind wing were at first alike. They are alike in ontogeny. They become progressively differentiated in all orders in an ascending series.

Wings were doubtless first broad at the base. The nature of their development from a marginal fold of skin requires this. Narrowing of the hinge line and of the wing stalk has progressed along with other specializations. The folding of the wings upon the back brought well known changes in the basal articulations, and longitudinal plication of the thin membrane at the hind border. Great expansion of this membrane followed in the hind wings of certain orders.

#### IV. VEIN FLUTING

The wing was at first flat, or perhaps gently arched upward and somewhat concave beneath. Contraction of the base threw it into folds there, and certain of these folds have had a degree of permanence. There resulted two principal elevations corresponding to the bases of the two primary groups of tracheæ, with a depression at the base of the median vein lying between.

In support of the cutting edge, the costo-radial group of veins became consolidated and stiffened by scleritization and by furrowing. Costa, Subcosta and Radius were firmly united at base (and often at tip as well), with the subcosta settled into the bottom of the furrow between the other two and braced against them. These three veins strongly conjoined support the wing as the mainmast supports a sail. Behind this support in the more primitive Palaeodictyoptera a full complement of forking veins extended across the field. The forks exhibit only such mutual adjustment as competing tracheal branches show.

At the rear of the wing base a free-floating support, formed by cubito-anal conjunction and scleritization, is generally well developed; but its veins are less constant in their relations. Always the vein R1 is convex to the upper side, and generally Cu1 is also. The weak base of the median vein lies in the hollow between.

The principal forks of these main veins originally lay farther out toward the middle of the wing, and the more or less numerous terminal forks often tended to fall into a fluted arrangement

alternately high and low, convex and concave. Wing fluting was characteristic of many of the older fossils. It has continued and has reached its maximum of development in modern mayflies. They stiffened the wing by fluting as a fan is fluted, and made little use of crossveins for wing-bracing. One may easily demonstrate the effectiveness of fluting by trying to fan himself with a sheet of plain paper, and then fluting it and fanning again. The fluting increases rigidity.

The fluting was of necessity incomplete at first, for when fluting begins forks are in the way. They flatten the surface; the conjoined veins cannot be convex and concave at the same time. Forks stood in the way of this sort of wing strengthening; and the simplest way of improvement lay in pushing them toward the wing base out of the way. Modern mayflies have perfected this process that was already well begun by Permian Ephemera. In the fossils the forks are farther out on the wing than in recent forms, and in the latter they recede until in the most specialized mayflies all are either crowded to the very wing base or detached. Thus the fluting was extended from the margin inward.

When principal forks are deepened to the wing base, then the number of veins in the wing appears to be increased. La-meere, observing their number and the regularity of the fluted arrangement into which they have fallen, evolved a theory of vein origin of very attractive simplicity. He conceived of a primitive wing with the veins all double, the anterior branch of each convex and the posterior, concave, following each other in perfectly regular order. Thus the convex costa had its concave subcosta; radius, its subradius, the radial sector (Rs); media, its submedia (M3+4); cubitus, its subcubitus (Cu2); and the 1st anal, its subanal (2nd A).

That was a beautiful dream. Nature is not often so consistent in arranging the parts of a series—and with such materials! The things here involved are open tracheæ extended through the mouth of a flat wing sac, “gathered” at transformation to a narrow wing base, and thus thrown into folds.

This theory provides for the excess of long veins, but it forgets that the number of main tracheæ is not increased—in fact it

forgets about tracheæ altogether, or dismisses them as of no significance. It forgets also that this excess in number of veins is found only in a few orders that have made no special use of crossveins for wing strengthening and that have deepened the forks progressively with wing-fluting.

When one considers the extraordinary diversity of wing types found among fossil insects, it does not seem likely that in all orders the veins should always be in the same relations to folds so formed. Within a single line of evolution, as for example, the Ephemeroptera, relation of veins to flutings once established would not be likely to change. Professor J. H. Comstock, in pointing this out (*Wings of Insects*, 222-223), made a reasonable use of wing fluting as an aid to the interpretation of homologies.

This beautiful theory was easy of application—too easy, in fact. One thing only had to be kept in mind—the fluted surface!

But there are basic facts of wing origin and vein development to which theory must conform if we are to make any real progress.

After Lameere had that beautiful dream Tillyard had a venational nightmare. His subconscious fancy conceived a primitive insect wing that had only one convex vein (R1), but it had a full complement of concave ones. He published a picture of it (*Amer Jour. Sci.*, 9: 333, fig. 2, 1925). The other convex veins, he said, came later, *arising from the outer margin of the wing*, and gradually extending toward the wing root. Whence they came and what they were made out of and how they were supported in the making are no concern of this theory, according to which tracheæ came last of all. "They find their way into the veins."

Thus, untrammelled by reality, the air-distributing function of trachea during wing growth ignored, the archedietyon forgotten, development from the base outward reversed, we arrive at another very simple solution of a very complicated problem.

That we are not greatly helped toward an understanding of wing-fluting by such special creation theories, I have pointed out elsewhere (*Science N.S.* 25: 221). The wing was first smooth of surface, as the nature of its origin necessitates, and the first longitudinal ridging probably came at the wing roots with the narrowing and consequent crowding there. Lines of contraction

may be seen through the transparent sheaths of nymphal wings in the instars approaching metamorphosis. They remind one of the lines at the base of a "gathered" ruffle. The fluting of the outer portion of the wing was one line of later evolution.

#### V. VENATION PATTERNS

Selective segregation of the chitin in the formation of the framework of the wing has followed very diverse lines. Numberless venational ventures have been tried. A good many have succeeded well enough to have persisted down to the present day. Many more have failed, as the fossil records show. In all this diversity a few main trends appear, and only with these are we here concerned.

Everywhere the framework of venation shows a stiffened front border with close-set veins, and an expanded rear margin with outspread veins. Everywhere the lines of support for this framework proceed from two basal thickenings at the costo-radial and cubitoanal conjunctions of veins at the wing base, out toward the stigmatic area of the wing. At the front is stiffness; at the rear, pliancy; between is a thin basal area traversed by lines of torsion. This makes for sculling efficiency.

In the more primitive fossils the veins were almost as independent as were their antecedent tracheæ but mutual adjustments came in as the old archedictyon was dissolved and its substance reassembled on lines of greater utility. Sometimes it emerged as rows of hexagons. More often, especially in the narrower wing spaces, as parallel crossveins. Always it went toward further strengthening of some of the main veins.

A struggle for existence among the all-too-numerous crossveins ensued and certain of them, that chanced to stand in positions advantageous for support, were preserved. Strong transverse joinings of the longitudinal veins were the result. An outcurving line of crossveins connected the two basal vein-groups of the wing. It was the line of the arculus. Another crossline was the line of joinings connecting principal forks. I have elsewhere (N. Y. State Mus. Bull. 124: 223, 1907) spoken of this, and have called it the *cord*. It is a line of conjoined forks. Those crossveins that stood at the elbows of the forks had the advantage of

position and survived. They remain still as the named crossveins of Comstock's typical wing: *r*, *s*, *r-m*, *m*, and *m-cu*, present in the more primitive members of holometabolous orders.

Such was the mechanical adjustment when the primal forking of the veins was dichotomous. But there was, apparently from the beginning, another type, a pinnate\* type, in which the forks of the veins (and of their antecedent tracheæ) were arranged in a unilateral series. This is the Neuropteroid type. It reached its zenith in the Hemerobiidæ and Myrmeleonidæ.

The forks in this type extend obliquely outward and rearward, often downcurving, like the primaries of a bird's wing. Between the forks the surviving crossveins are arranged in gradate series. The result is a very beautiful wing, but not one of great efficiency; for there is too little thinning toward the hind border: too much material there still. Even a marginal vein persists—relict from the old wing-fold channel—where for efficiency the wing should be thinnest.

Primitive insect wings carried an excess of veins, and the general tendency, it now seems clear, has been toward vein reduction, together with vein differentiation. The best fliers have often the fewest veins. The chitin has been concentrated in a supporting framework of a few strong veins placed at the front where strength is needed for support. At the rear it has been spread out thin to form a tough and pliant membrane where breadth is needed for gliding. Progressive series in vein reduction may be found in most of the insect orders.

Fluting alone did not yield very efficient wings. Better wings were evolved when strong crossveins were developed, binding together the longitudinal veins in a strong yet flexible supporting framework.

#### VI. MAYFLIES AND DRAGONFLIES

A few words now about the two groups whose venation is most in dispute. Ever since Latreille put mayflies and dragonflies together in one order, SUBULICORNIA, it has been commonly held that they are closely related groups. I formerly shared in this

\* Better *pinnate* than *pectinate*; for the rays are appressed, oblique and arched as in *pinna*, a feather, and not apart, perpendicular, and straight as in *pecten*, a comb.

opinion, but further study has convinced me that both are very isolated groups, well apart from other insects and from each other.

They have a few very well known common features. Both groups have reduced antennæ, as Latreille's name for them indicated; but this is a departure from primitive conditions and may well have been a parallel development. Both groups have enormously developed compound eyes; but the eyes have little in common save what is common to insects generally. Both groups have a ten-segmented abdomen; but so had many unrelated fossils. Both have a certain curvature of the veins of the cubito-anal group that they share with several equally isolated fossil orders. Both groups hold their wings outspread and not folded on the back.

This last common feature on close inspection will reveal little affinity; for the wings of the two groups differ vastly in development, in mechanical arrangements, and in general evolutionary trends. The nymphal wings lie flat on the back in Ephemeroptera, inverted in Odonata. The hind wings tend to be reduced in Ephemeroptera, expanded in Odonata. They are coadapted to the fore wing in Ephemeroptera but remain free and independent in the Odonata. Huge dorsal longitudinal muscles propel the wings downward by uplift of the tergum in Ephemeroptera, while these muscles are lacking in Odonata and the down stroke of the wing is effected by direct pleural wing muscles. The base of the nymphal wing bears ingrowing callosities in Ephemeroptera that are lacking in Odonata. The stiffening of the wing has been chiefly by means of fluting in Ephemeroptera with hardly any use of special crossveins, while in the Odonata three strong cross bracings of the veins at arculus, nodus, and stigma are characteristic of the entire order. The area of the radial vein is expanded and that of the median reduced in Ephemeroptera, while these conditions are reversed in Odonata.

Other significant contrasts are seen in the life cycle; in mouthparts and feeding habits; in form and armature and segmentation of the tarsi; in gills and abdominal appendages; in hind gut and Malpighian tubules; in sex organs and copulatory apparatus of the male, etc. Here these only can be mentioned in passing.

The fluted condition of the insect wing was not primitive but secondary. It represents one of Nature's experiments in wing stiffening, tried out early, and largely abandoned, except in Ephemeroptera, where is reached perfection.

The veins in the Odonate wing are preceded by tracheæ—the usual tracheæ in their usual relations to an alar trunk at the wing base. The large tracheæ R, M and Cu fork well out in the wing as in more primitive insects. There is strict correspondence between veins and tracheæ over most of the wing in the more primitive members of the order, with progressive but very moderate departures therefrom as specialization proceeds.

When the veins are formed, they bend the contained tracheæ out of course. This happens where braces are developing, especially at areculus and triangle. This angulation increases with the approach of transformation. It shows how these wing braces arose. The bending is progressive. It reveals the lines of past evolution, and living adult forms still persist on the earth to illustrate each step in the shifting. Such consistent corroborative evidence from ontogeny and phylogeny is not to be lightly cast aside in behalf of a beautiful theory.

There are in this order several peculiarities of tracheation, as might well be expected in so isolated and peculiar a group of insects. The most noteworthy of these is the crossing of the trachea Rs over two branches of media. This occurs regularly in the suborder Anisoptera. The first formed exploratory tracheoles may or may not cross over, as Schmieder (*Entom. News*, 33: 257–303, 1922) has abundantly shown;\* but the definitive trachea follows the predetermined route unerringly.

This crossing occurs in ontogeny long before any veins are formed. If it occurred in phylogeny before the venation pattern was established, the crossing would necessarily be incorporated into that pattern. It is, of course, impossible that chitinized veins should cross; but it is not at all impossible for tracheæ to cross and for veins to be formed about them.

The most primitive arrangement of tracheæ in the Odonata, the one that accords best with the generalized representatives of

\* I hasten to acknowledge the error I once made in adducing ontogenetic evidence from tracheoles (*U. S. Nat. Mus. Proc.* 26: 706, 1903).

other orders, is that of the suborder Anisoptera, whose large nymphal wings are of considerable thickness. Apparently there is crowding at the front; for, as in saltatorial Orthoptera (whose nymphal wing cases are likewise inverted on the back), the area of the radial trachea is reduced, and that of the median, expanded.

Reduction occurs at both front and rear. The costal trachea atrophies. There is a single anal trunk and it is crowded forward against the base of the cubital stem. Translocation of branches may be traced, if one examine a representative series of the order. The branches of the anal trachea are transferred to the cubital, progressively as specialization proceeds and as the nymphal wings becomes narrower and thinner, until their dwindling remnants are all detached from their place of origin. Even so the trachea Rs has been transferred from the radial trunk to the median in Zygoptera. The explanation of all these translocations is *compression*. Tracheæ must remain open.

In the thinning of the wings of the slender zygopterous nymph, the trachea of the radial sector has apparently been pinched off and a new cut-off channel formed, joined it to Media. This could occur at ecdysis, when the tube is emptied of both gas and taenidia. Then the soft protoplasmic walls are easily expanded. Then with the old passage blocked by compression, a new one might be formed. Following aeration demand, as trachea seem to do in general, an outgrowth from Media would find the soft channel of the detached tip of Rs and unite with it. This is the explanation I offered in 1903 (U. S. Nat. Mus. Proc. 26: 711), and I see no reason for change.

Tillyard, while objecting to this explanation of the Zygopterous tracheal pattern, unwittingly provided the best of evidence for it (Linn. Soc. N. S. Wales, Trans. 40: 227, 1915) when he pointed out the old abandoned vein-channel in the subnodus of the Australian Diphlebia. This I have discussed elsewhere (Entom. News, 28: 171-173, 1917).

Tillyard has held that the condition of the trachea in Zygoptera is primitive and has disposed of the crossing of Rs in Anisoptera by calling it a "tracheal specialization"; but he has not pointed out any of the usual signs of specialization, such as be-

ginning and trend, with more or less gainful progress. How could a branch on the posterior side of the median tracheal stem detach itself therefrom and reattach itself to the more distant radial stem on the other side? Or, how could a well established branch of the median trachea be dispossessed of its field by an invading distant branch of radius? Either procedure is to me unthinkable.

He argues that if the bridge vein were a secondary development, then some fossils should show it incomplete. To this reply may be made that fossil evidence, like that of tracheation, is good for what it shows not for what it does not show. Fossils (and the more generalized recent forms as well) show the bridge indifferently developed at its proximal end, and attaching forward or rearward; to M1 + 2 in some groups and to M3 in others.

A point of departure for a new interpretation of Odonate venation was found by Tillyard when he discovered the fossil, *Kennedyia mirabilis*. This for him at once solved the whole problem. With all considerations of developmental processes discarded, he was able to see in this extraordinarily specialized form the ancestral characters of modern Odonata; and that in spite of its long-stalked wings, its high differentiation between veins and membrane, and its few crossveins in fine mutual adjustment!

One little veinlet at the very base of the wing was for him the key. This veinlet, one cell long, he called Cu1. It does not look like Cu1, but he thought it to be convex and a convex Cu1 was needed here to fit his version of Lameere's theory. It seems strange that he did not deem it necessary to supply tests of a sort that he himself has demanded elsewhere: (Roy. Soc. Tasmania, Proc. of 1910, p. 17) "Where is the evidence that such a vast change as this ever took place, and where are the intermediate forms to be found?"

Tillyard's interpretation assumes that about nineteen-twentieths of the distal portion of vein Cu1 has disappeared and left no trace — has fused with Cu2 in a series wherein no signs of fusion from the margin inward are ever seen, nor approximation of vein tips looking toward coalescence; not even in related orders, recent or fossil. This interpretation is fantastic.

Or, if the thought be, that vein Cu1 has all atrophied except this little basal vein while adjacent veins and crossveins show no signs of reduction or of readjustment, that is equally preposterous.

A simpler explanation of this little vein lies near at hand. The portion of the wing in which it lies remains longest an open sac. The gathering up from the rear crowds the tracheæ of the cubito-anal group forward. It might well be that the cubital trachea was pushed ahead of the anal into the midbasal space. The weak vein formed about it in that case would be the cubital stem, with its fork farther out in the wing where it belongs. The stray vein behind it would be the ascendent anal.

A veinlet of this sort occurs in the Meganisopteran genus *Typus* at the posterior side of the midbasal space. A similar veinlet appears in *Oligotypus* at the anterior side of this same space. These are figured together by Carpenter on the same page (*Amer. Journ. Sci.* 21: 107, 1931). Both are probably due to a common cause—the gathering up of the wing base preparatory to transformation. I think that they should be interpreted alike. Both represent short fusions just beyond the base: M with Rs in *Typus*; Cu with A in *Oligotypus*. There is no reason whatever for assuming loss of vein tips by fusions the whole wing length.

The two suborders of Odonata, Anisoptera and Zygoptera, are very remote in origin, as shown in the nymph by different type of a respiratory apparatus and in the adult by different type of head, and by want of homology in the component parts of the accessory genitalia of the male. That they arise from common stock is shown by the common form of labium in the nymph and of venation pattern in the adult. Tillyard has sought to show by palaeontological evidence that the Zygoptera with reduced venation are very primitive but he has only succeeded in showing that they are very ancient.

Much of the primeval fluting has been preserved in Odonata; indeed, it has been both preserved and improved upon. But it is no longer the simple fluting called for by Lameere's theory. Principal veins are no longer consistently concave or convex. In *Aeschna*, for example, costa is convex to the nodus and con-

cave beyond. M4 is concave in the middle and convex to both ends. With veins ajog on the bends into which they forced the tracheæ there came about of necessity a partial levelling at the junctions, giving ups and down in the course of single veins.

#### VII. SUMMARY

I trust I have made clear my belief that in studies of insect phylogeny all features of wing development should be taken into account and given due weight:—

1. Tracheæ, when dealing with any group that has living representatives. The principal reason for considering trachea is because veins develop about them. Also when well preserved, by their shiftings of position they retrace in ontogeny the evolution of the vein pattern in each group. This, confirmed by adult wings showing the same shifts, yields consistent and satisfactory evidence of the course of evolution. Unfortunately, for extinct groups only phylogenetic evidence is available, and that is often very scanty. However, in the more generalized fossils, tracheæ leave their traces in the manner of forking of veins. Also, when fusions have occurred often there remain oblique veins to indicate conjunctions.

2. Principal veins, their number, type and extent of branching and relative interdependence.

3. Cross-veins. These are much a part of the wing as are long veins. Their emergence from the archedictyon is progressive. Where numerous they are individually insignificant, but when few and strong they become major parts of the wing mechanism.

4. Vein patterns, as manifest in the dichotomy of main veins, and in the connections established between them by means of crossveins.

5. Fluting: convex and concave furrowing; a means of wing stiffening in absence of strong crossveins; very important when once established in a single series, but undoubtedly secondary as the nature of the wing at its origin necessitates, and not necessarily holding individual veins to the same levels in different types of wing. Along with fluting should be considered other

changes of level due to the development of lines of flexion, and lines of bracing.

When all the methods of comparative anatomy have been applied to the study of the older fossil insects the evidence will still be scanty enough, in all conscience, and not an adequate basis for cocksure pronouncements. The surface of the fossil record has only been lightly scratched.

Even yet there has been no thoroughgoing investigation of the development of a nymphal wing in any species, and no study at all of fluting to determine the limits of its dependability as a guide in studies of phylogeny. In such researches the methods both of observation and experiment must needs be applied.

I would not conclude this article without paying tribute to the excellent palaeontological work of my three esteemed Neo-Adolphian colleagues, Tillyard, Martynov, and Carpenter, with whose application of Lameere's theory I disagree. Their contributions to the knowledge of fossil insects are very great. New facts they have contributed in a large measure; and the enduring edifice of science is built on facts.